



Short Communication

Positive relationship between herbaceous layer diversity and the performance of soil biota in a temperate forest

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ABSTRACT

The current decline in biodiversity is particularly pronounced in the herbaceous layer of forest ecosystems. We explored the relationship between a naturally occurring plant diversity gradient in the understorey vegetation of a deciduous forest and several above-and belowground ecosystem processes. We show that particularly soil microbial parameters and microarthropod densities are positively correlated with plant species richness. These results confirm recent findings in grassland ecosystems and highlight the intimate interconnectance between the diversity and functioning of above-and belowground compartments. We conclude that irrespective of a potential causal relationship between plant species richness and belowground processes, it is essential to consider the performance of soil biota in order to understand the relationship between herbaceous layer composition and ecosystem function.

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Anthropogenic alterations of Earth's ecosystems and their functions are substantial and multifaceted (Vitousek et al., 1997). One major current global change phenomenon is the loss of biodiversity (Pimm et al., 1995; Sala et al., 2000), being particularly pronounced in the herbaceous layer of forest ecosystems (Gilliam, 2007). As the functioning of forest ecosystems essentially relies on the composition and diversity of the herbaceous layer (Gilliam, 2007), the question arises how the latter is linked to soil biota performance and processes (Wardle et al., 2004; Wardle, 2006; Eisenhauer et al., 2010a). Most knowledge on the relationship between plant diversity and the performance of soil biota is based on manipulative semi-natural grassland experiments (Spehn et al., 2000; Hedlund et al., 2003; Eisenhauer et al., 2009a). In forest ecosystems, impacts of tree identity or litter diversity on soil biota have been studied (Keith et al., 2008; Wardle et al., 2008). Only few

studies considered the effects of plant diversity of the herbaceous layer on soil microbial communities (Carney and Matson, 2005; Royer-Tardif et al., 2010; Gilliam et al., 2010). Here, we explore the naturally occurring gradient in herbaceous layer plant species richness (PSR) and the linkage to above- and belowground processes and organisms.

This study was conducted in a deciduous forest in southwest Alberta (51°2'N, 115°4'W). The dominating tree species in the investigated forest was trembling aspen (*Populus tremuloides*) interspersed with some balsam poplar (*Populus balsamifera*). The herbaceous layer was dense and mainly consisted of herbs (e.g. *Aster conspicuus*, *Epilobium angustifolium*, *Delphinium glaucum*, *Heracleum lanatum*), roses (*Rosa acicularis*, *Rosa woodsii*) and grasses (e.g. *Bromus* sp., *Danthonia* sp., *Agropyron* sp.) (Fig. 1; see Eisenhauer et al., 2009b for plant species list). The soil was classified as orthic grey luvisol (Karkanis, 1972). Mean annual precipitation at the study site is 625 mm and mean annual temperature in the organic layer 3.8 °C (Mitchell, 1974).

In August 2004 and 2007, we randomly selected 10 locations per sampling campaign, spaced >20 m apart, where we investigated

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Fig. 1. Photograph of the studied aspen forest in southwest Alberta (Canada) in 2004 showing the dense herbaceous understory vegetation, one exemplary plot, and N. Eisenhauer assessing plant community traits (Photo by K. Yee).

plots of 0.5×0.5 m (Fig. 1). Plots studied in 2007 were >5 m from the plots sampled in 2004, and plots were generally >20 m from the forest edge. We determined PSR of the herbaceous layer, plant species-specific coverage (% coverage, modified after Daubenmire, 1959), as well as plant density by counting plant tillers. Forbs were identified to species level, whereas grasses were grouped together. Nevertheless, we will use the term PSR in the following, since forbs made up 72 and 75% of the plant biomass in 2004 and 2007, respectively. PSR in the plots varied between 9 and 14 species in 2004, and between 6 and 12 species in 2007. We harvested aboveground plant biomass by cutting the vegetation <10 mm above the soil surface level. We then removed plant litter materials, and both plant and litter materials were dried to constant weight (80°C , 48 h).

Adjacent to each of the plots of the vegetation survey, we took two soil cores using a metal corer (diameter 5 cm) to a depth of 15 cm. One of the cores was used to determine soil microbial parameters, and the second to extract soil microarthropods by heat (Macfadyen, 1961). Extracted soil microarthropods were stored in 70% ethanol and identified as far as possible (species to family level). Microbial respiration and biomass were measured using an O_2 microcompensation apparatus (Scheu, 1992). Basal respiration was determined without addition of substrate; microbial biomass was calculated from the respiratory response to D-glucose (Anderson and Domsch, 1978; see Eisenhauer et al., 2007 for details).

Data were log-transformed to meet the requirements of regressions, if necessary (plant density in 2007). Regressions were performed between PSR and plant, microbial and microarthropod performance parameters listed in Table 1 using STATISTICA 7 (StatSoft, Tulsa, USA). In order to illustrate results of both years in a comparable way in the figures, variables were standardized, i.e. minimum values ascribed “0” and maximum values “1”. According to largely consistent relationships, we also discuss marginally significant regressions (Table 1).

Aboveground plant biomass was not correlated with PSR (Table 1). There was a negative relationship between PSR and plant coverage in 2004 but not in 2007. Plant density was positively correlated with PSR in both years (Fig. 2A). In 2007 there was a negative correlation between PSR and litter biomass (Fig. 2B). Microbial biomass (Fig. 2C) and basal respiration (Fig. 2D) were

Table 1

Table of R^2 - and P -values of the regressions between plant species richness of the herbaceous layer vegetation and plant performance parameters, litter biomass, soil microbial parameters, and the density and diversity of soil microarthropods in 2004 and 2007 (dominant taxa; see Eisenhauer et al., 2007 and Straube et al., 2009 for details).

	2004			2007			
	R^2	P		R^2	P		
Plants							
Plant biomass	–	0.08	0.4185	–	0.00	0.9492	
Plant coverage	–	0.33	0.0853	↓	+ 0.06	0.4962	
Plant density	+	0.30	0.0929	↑	+ 0.65	0.0047	↑
Litter biomass	+	0.07	0.4469	–	0.67	0.0036	↓
Microorganisms							
Basal respiration	+	0.40	0.0508	↑	+ 0.65	0.0050	↑
Microbial biomass	+	0.30	0.0983	↑	+ 0.36	0.0689	↑
Mesofauna							
Collembola (total)	+	0.36	0.0674	↑	– 0.23	0.1653	
Isotomidae	+	0.28	0.1143	–	0.19	0.2122	
Onychiuridae	+	0.31	0.0940	↑	+ 0.11	0.3536	
Oribatida (total)	+	0.21	0.1887	+	+ 0.33	0.0850	↑
Oppiidae	+	0.19	0.2029	+	+ 0.41	0.0451	↑
Brachythoniidae	+	0.19	0.2121	+	0.13	0.4318	
Total density	+	0.24	0.1482	+	0.14	0.2829	
Total diversity	+	0.52	0.0184	↑	– 0.10	0.3730	

Significant ($P < 0.05$) and marginally significant ($P < 0.1$) effects are given in bold. $N = 10$, ↑ = increase with increasing plant species richness, ↓ = decrease, +/- indicate the tendency of the relationships (according to positive or negative correlation coefficients).

positively correlated with PSR. Collembola density and PSR were positively correlated in 2004 (Fig. 2E), primarily due to high density of Onychiuridae, but not significantly correlated in 2007. In 2007 there was a positive correlation between PSR and Oribatida density (Fig. 2F), which was mostly due to a positive correlation between PSR and the density of Oppiidae. While there was no correlation between PSR and total density of soil microarthropods, total diversity of microarthropods was positively correlated with PSR in 2004.

Forest biodiversity is largely a function of the herbaceous layer vegetation (Gilliam, 2007). The results of the present study suggest a positive relationship between herbaceous PSR and plant density, soil biota performance and functions. The positive correlation of PSR with microbial biomass, basal respiration and -in some years- positive relationships between the density of Collembola and Oribatida and a negative correlation between litter biomass suggests that litter diversity stimulated decomposer activity and thereby decomposition processes. Of course, correlations do not necessarily reflect causal relationships, and above- and belowground parameters may be driven by other abiotic or biotic conditions (Rusek, 2000; Hooper et al., 2000). However, we found no significant relationships when we tested PSR against distance to forest edge, tree and shrub coverage and soil water content (data not shown; see Eisenhauer et al., 2007).

Recent findings in temperate grassland point to an intimate relationship between the diversity and functioning of above- and belowground compartments of terrestrial ecosystems. While soil biota essentially rely on the quality of plant derived resources (Wardle et al., 2004), plant performance is driven by the activity and diversity of decomposers (Eisenhauer et al., 2009c, 2010b, 2010c). Results of the present study suggest a similar above–belowground interconnectance in forest ecosystems, reinforcing previous studies on soil microbes (Carney and Matson, 2005; Royer-Tardif et al., 2010; Gilliam et al., 2010). We conclude that, irrespective of a potential causal relationship between PSR and

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